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Do white-tailed deer and the exotic plant garlic mustard interact to affect the growth and persistence of native forest plants?

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ABSTRACT

Herbivores and invasive plants strongly affect the persistence of individual species and the overall composition of forest plant communities. Although their impacts are usually studied separately, they often co-occur with potential synergistic effects on native plants. We used a 2 × 2 experimental design replicated across five locations in southern Wisconsin to assess the separate and combined effects of herbivory by white-tailed deer (*Odocoileus virginianus*) and competition from the weedy invader *Alliaria petiolata* (garlic mustard) on five native species. Deer and *Alliaria* often reduce the growth and survival of native plants in these forests. A fenced exclosure erected at each site surrounded one of two pairs of adjacent plots densely occupied by *Alliaria*. We cleared one plot (in- and outside each exclosure) of *Alliaria* and then planted seedlings of the native species into all four plots. Species were chosen to display different functional traits (*Aster lateriflorus*/*Symphyotrichum lateriflorum*, *Carex blanda*, *Geranium maculatum*, *Quercus rubra*, and *Uvularia grandiflora*). We then monitored native seedling growth and survival for 13 months. Deer access depressed survival and branching in *Uvularia,* growth in *Geranium* and *Quercus*, and tillering in *Carex*. The presence of *Alliaria* reduced height and tillering in *Carex* and *Geranium* but increased branching, reproduction, and survival in *Uvularia*. Thus, *Alliaria* may sometimes act to protect taxa like *Uvularia* sensitive to deer herbivory. *Alliaria* reduced the growth of *Carex*, *Geranium*, and *Quercus* significantly more in the absence of deer. Such interactive effects suggest that when deer do not restrict growth, plants grow larger to a point where *Alliaria*'s competitive effects increase. The impacts of both deer and *Alliaria* varied by species and trait. Species experiencing regional declines (e.g., oak seedlings and the lily, *Uvularia*) were more affected by deer than by *Alliaria*. Oak seedlings suffer particularly from *Alliaria* competition when deer are absent. Managers seeking to sustain deer-sensitive species should first work to reduce deer densities before seeking to control weedy plant invasions. *Alliaria* reduced growth more in species that tolerate deer browsing (*Carex* and *Geranium*). These differential responses argue for tailoring local deer and weedy plant control efforts to the taxa of concern. Deer and weedy plants have cumulative effects on native plant species. Interactions between their effects will become more important as their populations and impacts increase.

1. Introduction

Long-term studies of temperate forest plant communities reveal surprisingly large declines in diversity (Rooney and Dress, 1997; Waller and Rooney, 2004; Rooney et al., 2004; Rogers et al., 2008). Two of the several mechanisms associated with these declines are high rates of herbivory by white-tailed deer (*Odocoileus virginianus*) and invasions of weedy exotic plant species. Deer selectively browse native species, shifting the composition of forest understory communities away from palatable and preferred species (including many lilies, orchids and lobeliads – Miller et al., 1992) toward species that can resist or tolerate browsing (including certain ferns and many graminoids – Wiegmann and Waller, 2006). These impacts, which reduce the cover and diversity of native plants including tree seedlings, can greatly alter forest composition and successional trajectories with cascading effects on nesting birds and other animals (Rooney and Waller, 2003; Eschtruth and Battles, 2008; Horsley et al., 2003; Waller et al., 2009; Côté et al., 2004; Rooney et al., 2004; McShea and Rappole, 2000; Rooney and Dress, 1997; Augustine and McNaughton, 1998; Ostfeld et al., 1996; Russell et al., 2001; DeCalesta, 1997; Conover, 1997). Deer herbivory can also restructure plant communities (Suzuki et al., 2012), magnify the impacts of climate change (Zarnetske et al., 2012), and facilitate exotic plant invasions (Vavra et al., 2007; Waller et al., 2009; Eschtruth and Battles, 2008; Knight et al., 2009). Given that both deer and invasive plants have significant impacts on plant communities,

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it behooves us to explore their separate and combined impacts on native plant species.

The European biennial garlic mustard (*Alliaria petiolata*) is one of the most invasive and abundant non-native plants in the forests of southern Wisconsin (Rogers et al., 2008). Garlic mustard reduces native plant germination, growth, and diversity by releasing secondary compounds (allelopathy) that diminish and disrupt mycorrhizal associations, altering soil chemistry, and outcompeting natives for space and resources (Rodgers et al., 2008; Meekins and McCarthy, 1999; Stinson et al. 2006; Roberts and Anderson, 2001; Prati and Bossdorf, 2004; Murphy 2005; Barto et al., 2010; Cipollini and Gruner, 2007; Stinson et al., 2006; Wolfe et al., 2008; Wixted and McGraw, 2010; Lankau, 2011). Deer could accentuate these impacts to native plants via "apparent competition" if deer and other herbivores avoid *Alliaria* to feed preferentially on native species. Studies that have sought to link deer herbivory to the impacts of *Alliiaria* have focused on how deer tend to avoid it and how this, in turn, may allow deer to facilitate invasions (Eschtruth and Battles, 2008; Knight et al., 2009; Vavra et al., 2007). We are not aware of research that explicitly investigates how deer and garlic mustard interact to affect native plant performance, though Nuzzo et al. (2009) and Vavra and Wisdom (2007) noted the need for such studies.

Here, we present results from a study designed to evaluate the separate and combined effects of deer and *Alliaria* on seedlings of five native plant species: calico aster (*Aster lateriflorus* or *Symphyotrichum lateriflorum*), eastern woodland sedge (*Carex blanda*), wild geranium (*Geranium maculatum*), largeflower bellwort (*Uvularia grandiflora*), and seedlings of northern red oak (*Quercus rubra*) (henceforth referred to by their genus names). We used seedlings of these species as 'phytometers' to provide standardized and comparable measurements of plant success across treatments (Alverson and Waller, 1997; Fletcher et al., 2001; Ruhren and Handel, 2003). We specifically sought to evaluate the relative strength of these impacts and to identify whether deer and *Alliaria* have synergistic, additive, or compensatory effects on native plants growing in southern Wisconsin forest understories. Because exotic earthworms also affect native forest understory plants in our region (Nuzzo et al. 2009), we evaluated their effects as well. Improving our understanding of how deer and *Alliaria* act to affect the performance of native forest plants improves our ability to manage these habitats by focusing resources efficiently toward the most significant threat.

We designed a simple factorial experiment to determine the species-specific responses of five native species to removing deer and *Alliaria*. We predicted that: (1) *Uvularia* and *Quercus* would benefit more from deer removal than from *Alliaria* removal treatments; (2) *Carex* would benefit more from *Alliaria* removal than deer removal; and (3) *Geranium* and *Aster* would benefit similarly from *Alliaria* and deer removal as they are neither strongly preferred nor avoided by deer.

2. Materials and methods

2.1. Study species

We chose particular species to represent a range of historical population trajectories and probable responses to deer herbivory and *Alliaria* invasion. *A. lateriflorus* (*S. lateriflorum*) has increased over the past 50 years, *G. maculatum* has sustained an even population, and *C. blanda*, *Q. rubra*, and *U. grandiflora* have all declined (Table 1). Both *Uvularia* and *Quercus* are favored by deer (Augstine and McNaughton 1998; Strole and Anderson, 1992). Oak seedlings repeatedly browsed by deer often die (Waller and Alverson, 1997; Rooney and Waller, 2003; Waller et al., 2009). In contrast, graminoids deter herbivory via their high silica content and/or tolerate deer herbivory by resprouting vigorously from low meristems (Rooney and Waller, 2003). We presume that *Carex* has declined in response to increasing shade in southern Wisconsin forests as graminoids have thrived over the past 50 years in heavily browsed forests in northern Wisconsin (Côté et al., 2004; Rooney et al., 2004; Horsley et al., 2003). The effects of *Alliaria* similarly vary over species (Rodgers et al., 2008). Stinson et al. (2007) found tree seedlings and graminoids to be adversely affected by *Alliaria* while herbs and shrubs displayed few negative effects.

Table 1
Growth traits measured in each of the five native 'phytometer' species. "Long-term trend in abundance" reflects the 50 year region-wide shift in total abundance as reported by Rogers et al. (2008).

Species Long-term Trend:	*Aster* Increased	*Carex* Decreased	*Geranium* Stable	*Quercus* Decreased	*Uvularia* Decreased
Traits					
Height	x	x	x	x	x
# Leaves			x	x	
# Stems	x				x
# Nodes	x				
# Branches				x	x
# Culms		x			
Longest leaf	x	x	x		x
Basal diameter				x	

2.2. Study sites

We chose five study sites distributed across four state parks (SPs) in south central Wisconsin: New Glarus Woods SP, Blue Mounds SP, Governor Dodge SP (with upland and lowland sites), and Tower Hill SP. The understories at all these sites were dominated by *Alliaria*, *Circaea lutetiana*, and *Parthenocissus*. Deer are fairly abundant (10–12/km^2, Wisconsin DNR, 2012) reflecting their current abundance in the region. *Alliaria* cover ranged from 28% to 44% across these sites. As parks, all sites are open to public access via roads and trails and managed in similar ways (i.e. with some deer hunting in recent years, minimal logging and fire, and limited invasive species control efforts). They also experience similar climates and landscape conditions. All study plots were located at least 25 m from any trail or road in deciduous forests.

Carex occurred in the background vegetation at all sites and *Aster* at all except New Glarus. *Geranium* was present in the plots at Blue Mounds and the upland Governor Dodge site. *Uvularia* only occurred in the background vegetation at NewGlarus. No *Quercus* seedlings occurred in the sampled background vegetation at any of the sites despite the fact that mature red oaks occur at all these parks.

2.3. Treatments and experimental design

We assessed the effects of deer herbivory and competing *Alliaria* populations using a 2 $\times$ 2 factorial design that either allowed or prevented both deer access (via fenced exclosures) and local competition from *Alliaria* (via weeding). At each of the five sites, we erected a ~20 m $\times$ 20 m fenced exclosure in early May 2010 using 2.3 m tall polypropylene anti-deer fencing (www.gemplers.com) nailed to existing trees and staked into the ground. We regularly maintained these exclosures throughout the study period. Although a deer breached the Tower Hill exclosure between June and July 2010, only oak seedlings were damaged and these individuals were excluded from analysis. Exclosures provide an effective way to evaluate deer impacts on forests (Alverson and Waller, 1997; Horsley et al., 2003).